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Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*)

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Abstract

Results of a 4-year study in Sangay National Park, Ecuador, indicated that the mountain tapir *Tapirus pinchaque*, consumes a wide variety of woody and non-woody plant taxa primarily as a foliose browser, and has a preference for some nitrogen-fixing plants. The more closed-cover Andean forest and chaparral habitats contain a greater abundance of mountain tapir-favoured food than the more open grassland paramo, riverine meadow, and pampas vegetation types. Andean forests are considered the most critical habitat for the survival of this tapir because of their provision of cover and food. Field observations and results of faecal germination experiments show that the mountain tapir assists in the successful seed dispersal of many species of Andean plants. Significant regressions between: (1) seed germination and (2) both the natural logarithm (ln *e*) of the preference ratio and the dietary abundance of food species indicate a mutualism between the mid to high montane-dwelling mountain tapir and the plants it consumes. A significant relation during the past 2 to 3 million years is proposed between: (1) the crossing of the Panamanian Isthmus and the occupation of the mid to high northern Andes by ancestors of the mountain tapir, and (2) the rise of the Andes and formation of the montane forest and paramo ecosystems above *c*. 2000 m elevation.

Key words: Andes, diet, dispersal, Ecuador, evolution, faecal analysis, germination, habitat, mountain tapir, mutualism, *Tapirus pinchaque*

INTRODUCTION

The mountain tapir is a solitary perissodactyl that inhabits the cloud forests and paramos in the northern Andes at *c*. 2000–4500 m elevation (Schauenberg, 1969). While camelids such as vicuñas and guanacos inhabit the dry puna to the south, mountain tapirs are associated with the moist, spongy paramo biome unique to the northern Andes. With fewer than 2500 individuals remaining, the species is considered endangered. Population declines are a result of habitat loss due to agrarian expansion and associated hunting pressure (Thornback & Jenkins, 1982; Downer, 1995, 1996*a*,*b*, 1997; Baillie & Groombridge, 1996).

Other extant tapir species consume plants whose seeds germinate from their faeces (Howe & Smallwood, 1982; Janzen, 1982; Williams, 1984; Bodmer, 1990*a*, 1990*b*, 1991; Rodrigues, Olmos & Galetti, 1993; Olmos, 1997). Viable seeds pass through the post-gastric digestive system of mountain tapirs and successfully germinate under appropriate climatic and edaphic conditions (Downer, 1995, 1996*a*,*b*). In contrast to ruminant digesters, the monogastric tapir passes through its gastrointestinal tract many more intact seeds that are capable of germination (Janis, 1976; Bodmer, 1989, 1991). Similarly, leafy material is not thoroughly decomposed and contributes substantially to the formation of humus (Ricklefs, 1979), in which the more complex organic compounds remain longer in the soil before final decomposition, thus helping to build soil structure.

The mountain tapir may have co-evolved and become co-adapted with many Andean plants through the formation of mutualistic relationships, such as occurs between pollinating birds, bats, and insects, in which plants provide animals with nectar (Ricklefs, 1979). In the mountain tapir, however, a particular nutritional need may be fulfilled by the plant, the seeds of which it successfully disperses.

Because populations of the endangered mountain tapir are declining at a rapid rate due to hunting, habitat destruction, and fragmentation (Baillie & Groombridge, 1996), information on the survival requirements and ecological importance of this species is urgently needed to design and implement an effective

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conservation strategy (Downer, 1997). Occasional observations of the mountain tapir in the field or in zoos have been made since its discovery in 1829 (Roulin, 1829; Goudot, 1843) and additions to existing knowledge were made by Schauenberg (1969), but to date, no intensive ecological study of this species in the wild had been conducted. For this reason, dietary composition and dispersal of seeds by the mountain tapir was examined as part of a study to determine individual home range, annual migration, habitat use, and social behaviour (Downer, 1996).

Mutualistic co-evolution between the mountain tapir and the Andean plant individuals and communities in which it lives was also tested. The abundance of favoured plants in the mountain tapir's diet was correlated with a quantitative assessment of their dispersal in faeces of the mountain tapir. These results are related to a synchronism between two well-known geological and evolutionary events: (1) the connection of Central and South America by the Panamanian Isthmus; (2) the rise of the Andes above 2000 m elevation – both occurring about 3 million years ago. It is hypothesized that both of these events coincide with the entrance of a common tapir ancestor from Central to South America and with the subsequent split of *Tapirus pinchaque* and *Tapirus terrestris*. This also then relates to the extinction of species of megafauna that had thrived in South America before the connection of the Panamanian Isthmus, and whose niches were subsequently occupied by tapirs, horses, bears, and other megafauna of northern ancestry (Janzen & Martin, 1982).

STUDY AREA

The 6 × 9 km (54 km^2) chief study area is in the Culebrillas sector of the 517 725-ha Sangay National Park (Zuñiga, Carrillo & Pacheco-S., 1992; Mena, Ulloa-Ulloa & Herrera-MacBryde, 1997) in Ecuador (*c*. 2°S, 78°30′W), *c*. 3 km north-west of Sangay Volcano (Downer, 1996*a*, fig. 2). It lies at 3300–4200 m elevation, and is composed of Andean forest, ecotonal chaparral, and paramo habitats. The forest has 2–4 m of precipitation annually and a temperature range of 6–12 °C, whereas paramo has 1–2 m of yearly precipitation and a temperature range of 3–6 °C (Holdridge *et al*., 1971), although freezing temperatures occasionally occur in the uppermost 'elfin' forests and paramos. Snow or hail can occur as low as 3500 m a.s.l. in the study area, and the volcano may be covered to its base with snow during July. Culebrillas experiences rain year-round, and even during the dry season (October–January) storms frequently arise, usually from the Amazon Basin (Cañadas-Cruz, 1983; Hoy, 1991).

To the west of Culebrillas, the land is occupied almost exclusively by pastoral Puruhaes and mestizos, who raise cattle and sheep and cultivate potatoes, onions, wheat, carrots, and other vegetables. To the east lies the Amazon Basin, which receives water from Culebrillas. Both the livestock of traditional communal organizations and of the Spanish haciendas invade the park. In addition, the dwarfed forests present in the study area are periodically devastated by ash and cinder, or even occasionally by lava erupting from the Sangay Volcano, among the world's most active (Lewis, 1950; Macey *et al*., 1976). The habitat of the mountain tapir consists of high-montane cloud forests (many of stunted growth form), paramo (a spongy and treeless biome characterized by moss, bushes, and grass unique to the northern Andes) (Ramsay, 1992; Mena *et al*., 1997), ecotonal chaparral, along with riverine meadow and pampas (Downer, 1996*a*).

The Andean forest includes the 'montane thicket' of Beard (1955) and the 'wet montane forest' of Macey *et al*. (1976) and generally contains trees 2–7 m high at an elevation of < 3500 m in the study area. The individual trees are laden with epiphytes, including mosses and ferns, and some of the trees have curving boughs. An atmospheric condensation on cloud forest vegetation augments moisture received from direct precipitation (Cavelier, 1991). Andean forest is the most indispensable habitat type for the mountain tapir, protecting the animal from icy storms and allowing concealment from predators (Downer, 1996*a*).

The ecotonal chaparral includes the 'elfin thicket' of Beard (1955) and grades between the earlier described Andean forest and the treeless paramo. This is composed of bushes and herbs with a scattering of trees, the vegetation being 1–2 m high. Many of the shrubs display small, densely clumped leaves and erect branches. Chaparral provides considerable shelter and abundant food for the mountain tapirs (Downer, 1996*a*, 1997). The elevation is 3500–3800 m.

Paramo occurs at > 3800 m in the study area. It is the treeless, moist, spongy grassland typical of the high, northern Andes. Leaves stacked as roseate columns occur in many of the plant forms, which include cushion-like hemispherical colonies of plants that resist freezing (Patzelt, 1985). During the wet season, mountain tapirs descend from paramo and shelter in Andean forests (Downer, 1996*a*). The riverine meadow borders streams and rivers passing through forest and paramo alike. It displays low-growing, herbaceous growth with a scattering of bushes and trees and is favoured for grazing and social interaction by mountain tapirs, especially since frequently visited mineral-seeps surface along the streams (Downer, 1995, 1996*b*).

Pampas are created from fires set by humans along the lower Culebrillas river plain and extends up along the broader tributaries. Here cattle have invaded the park and are the dominant herbivore; exotic herbs are imported as a consequence (Downer, 1996*a*: 55, fig. 5). Mountain tapirs rarely visit pampas, probably because of the danger they incur from hunters or bulls, in spite of the considerable food value, which is about equal to the other grassy habitat types, paramo and riverine meadow (Downer, 1997). In the study area, pampas occurs between 3300 and 3500 m elevation. This eroded and less species-diverse habitat type, in which the banks of many streams are undermined, threatens to take over vast areas of Sangay National Park if trends in livestock invasion are not reversed soon (Downer, 1995, 1996*a*,*b*,*c*).

MATERIALS AND METHODS

Dietary and habitat analysis

Field observation

Diets of mountain tapirs were determined by direct and indirect field observations. The plant species browsed and the parts favoured were noted. A total of 7 mountain tapirs were also tracked using radio-telemetry. These were 5 females and 2 males, all adults except for 1 sub-adult female. Approximately 3500 readings (Downer, 1996*a*), each with activity determination, were obtained during 3125 h of radio-tracking. Observation of browse selection occupied 211 h during all times of the year. Field studies included walking the trails of tapirs and observing which plants showed signs of use. A characteristic form of nipping plants, distinguishable from that of the pudu *Pudu mephistopheles*, brocket *Mazama rufina* or whitetailed deer *Odocoileus virginianus* (which lack upper incisors), as well as bite size and the presence of tapir tracks assisted in this task (Crawley, 1983; Acosta, Cavelier & Londoño, 1996).

Vegetative transects and identifications

Ten 2 × 50 m transects were sampled in the study area to document the plant species occurring in 5 habitat types: Andean forest, paramo, ecotonal chaparral, riverine meadow, and pampas. There were 2 transects per habitat type. These transects were established in areas of tapir use to represent typical mountain tapir habitat. Line sampling (2 m) occurred at each metre along the transect. Coverage and frequency of individual plants were recorded and noted for each species. Coverage by a species was represented as the percentage of the 2-m line (perpendicular to the transect axis) occupied by the species, while its frequency was the number of times individuals were encountered (Jacobs, 1974; Crawley, 1983). These were then converted into percentages for coverage and frequency for each species in relation to all species. Summed together these produced a combined index (c.i. = percentage coverage + percentage frequency). This methodology is modified from Braun-Blanquet (1979) and Matteucci & Colma (1982). Verification of plants collected was made at the Missouri Botanical Garden Herbarium in St Louis and the Catholic University Herbarium in Quito.

Microhistological dietary analysis

Faeces of mountain tapirs ($n = 37$) were collected from the study area to equally represent all tapirs present. Several boluses were collected for each sample and care was taken to avoid soil or other types of contamination of the faecal samples. For a basis of comparison from which to identify dietary species, plant samples were obtained from the line transects described above, as well as from additional field collections. The analysis of defecated and live collected plant material was performed by M. B. Gilbert and T. M. Foppe using the microhistological techniques (Johnson & Wofford, 1983) of the Composition Analysis Laboratory at Colorado State University. These microbiologists quantified plant material in the faeces mostly to the genus level. Sometimes higher taxonomic categories were applied, e.g. either to family level (as with the Ericaceae, which here include *Vaccinium* and *Pernettya*) or as groups such as ferns, unknown forbs, flower parts, moss, arthropods (including shiny and colourful elytra of Coleoptera), grass seed, or composite, referring to an unidentified member of the Asteraceae. To provide *typical ingesta* for microscopic analysis, material samples of plant parts favoured by the mountain tapir (buds, fruits, seeds, tips of branches, terminal twigs, and younger leaves) were collected for slide preparation. Thus, a reference collection was established according to procedures described by Johnson & Wofford (1983).

I prepared 5 mounted slides for each of the faecal samples and for each of 270 plant species collected and identified in the Culebrillas study area. The faecal slides were classified as *typical ingesta*. After identifying distinguishing characteristics (mesophyll and cuticle) for each potential dietary grouping from mountain tapir habitat, each of the 5 slides for each faecal sample was examined by microscope. At 20 per slide, a total of 100 microscope fields of view were examined at 125 × magnification for each faecal sample.

In each field of view, each taxon group with 2 or more distinguishing characteristics was tallied both for presence and for percentage coverage of the field, providing a frequency per cent index and a coverage index. Summing coverage and frequency rendered a combined index, which could then be compared with the combined index of coverage and frequency resulting from the vegetative transects. The resultant data were tabulated as means with standard errors. Means were evaluated with Student's *t*-tests (Johnson & Wofford, 1983).

Preference ratios

The preference ratio is the proportion of the frequency of a given food item in the diet of the mountain tapir (beta value) divided by its frequency in the habitat (alpha value) (Jacobs, 1974; Crawley, 1983). The preference ratio shows the degree to which an animal selects a given food item relative to its availability, or frequency of encounter, in its habitat. Any value > 1 indicates that the tapir is seeking out this item in greater proportion to that predicted from its frequency in the habitat, while any value < 1 indicates the opposite.

Seed dispersal and mutualism

Faecal seed germination experiment field studies

Field notes, photographs, and collections of plantules were used to document the seeds that germinated directly from faeces in the wild. This information was then employed to obtain taxonomically correct identifications at herbaria both at the Catholic University, Quito, and the Missouri Botanical Garden, St Louis, and from published sources.

Germination experiments were conducted at the Instituto Nacional de Investigacion Agropecuario (INIAP) greenhouse located south of Quito, which has an elevation and a temperature range that closely matches the study area. A regime of daily watering comparable to the level of precipitation found in the study area (*c.* 2 m/year) was maintained. Eight faecal samples were used. These were gathered from different mountain tapir home ranges, including those of radio-collared and of uncollared tapirs, to avoid pseudo-replication. Only faeces that were not mixed with native soil or did not have plantules sprouting from them were collected. From each faeces sample, a rounded lump of 32.8 cm was spread out thinly (*c.* 5 mm thick) in a furrow and then firmly covered with soil. Three planting plots were maintained for each of the 8 faecal samples ($n = 8$, with 24 treatments) that contained:

plot 1: *sterile soil* (oven heating according to standard procedures of INIAP and filtered to remove all seeds) in which the tapir faeces were planted at a depth of 6.35 cm;

plot 2: *a mixture of native soil* (filtered to remove all seeds) with tapir faeces planted at similar depth as in (1);

plot 3: *the unfiltered native soil only*, which served as a control plot without tapir faeces to determine which species of plant were present in the soil as viable seeds.

After 183 days of daily watering, the resulting seedlings were collected. Prior research provided evidence that most seeds passing through a gastrointestinal tract germinate 2–3 months after seeding, with some germinating 5 months later, which provided a justification for this schedule (Olmos, 1997). Those that grew from plot 1 were clearly identified as having come from the mountain tapir. Those seedling types that grew only from plot 2 permitted identification of symbiotic species seeded by the mountain tapir that required native soil to germinate. This procedure was used because of the frequent association between mycorrhizal fungi found in soils and germinating seeds that is required for successful seed germination (Daubenmire, 1967; C. Narvaez & K. Draeger, pers. comm.). It is less likely that plot 3 had contained seeds deposited by mountain tapirs, since this soil was selected from an area away from tapir faeces, trails, or home ranges. Though viable seeds can remain for a long time in the soil, it was felt that this procedure would eliminate many commonly occurring seeds found in the soils of the study area and dispersed by non-tapir means. A better identification of those seeds dispersed by the mountain tapir could then be obtained.

An index of mutualism

Product–moment correlation coefficients (Rohlf & Sokal, 1981; Sokal & Rohlf, 1981; Minitab, 1989) were calculated for all possible combinations of factors: (1) the frequency of the given plant in the tapir's habitat (alpha); (2) the frequency of this same plant in the tapir's diet (beta); (3) the preference ratio, and this as transformed to its natural logarithm, ln *e*, of this plant eaten by the tapir (PR and ln *e* PR); (4) the frequency of this plant as a successfully germinating seed in the tapir's faeces (GF). The correlation between (4) germination frequency and (3) preference ratio and ln *e*, used data from the 15 dietary plant groups, since only 15 such groups were represented in all 3 of the following: (a) microhistological dietary analysis; (b) vegetative transects; (c) faecal germination experiments and field studies. The direct correlation between (4) germination frequency and (2) dietary frequency used data from the 17 dietary plant groups represented in both (a) the microhistological dietary analysis and (c) the faecal germination experiments and field studies when the outlier value was included and from 16 groups without the outlier. Through these correlations, the hypothesis that a mutualism had evolved between the mountain tapir and the plants it more frequently consumes could be corroborated. If a significant correlation exists, then the mountain tapir would tend to disperse (4) to a greater degree the seed of those plants it most consumes (2) or preferentially selects (3).

RESULTS

Diet and habitat of the mountain tapir

Overview

Major food groupings for the mountain tapir in the Culebrillas study area and similar close areas demonstrate that the mountain tapir selects broadly among the plant taxa available (Table 1; Downer, 1996*a*: 50–51, table 1). Their diet includes a diversity of herbs, grasses, shrubs, and trees, their fruits and berries, twigs and a predominance of leaves. Of 28 plant families, Asteraceae ranked highest in the number of different species eaten, followed in diminishing order by Gramineae, Rosaceae, Cyperaceae, Fabaceae, Scrophulareaceae, and Valerianaceae. This ranking parallels the species diversity of families in the tapir's habitat (Table 1).

Certain groups, such as the aster *Gynoxys*, ferns, *Equisetum*, *Brachyotum* and *Gunnera*, account for a predominate portion of the diet. A comparison of each plant's frequency in tapir faeces (beta value) with its frequency in habitat (alpha value) indicates little statistical relation between these two factors (Table 2). The

Table 1. Numbers of species in families of Angiospermae: I, identified in study area; II, eaten by the mountain tapir *Tapirus pinchaque*; III, whose fruits/seeds are eaten by the mountain tapir. Culebrillas sector, Sangay National Park, Ecuador, 1990–93

Family	I	II	III
Subclass: Monocotyledoneae			
Bromeliaceae	2	2	2
Cyperaceae	12	10	10
Gramineae	23	23	16
Juncaceae	4	2	2
Subclass: Dicotyledoneae			
Apiaceae	7	3	3
Asteraceae	59	35	14
Brassicaceae (or Cruciferae)	5	2	2
Campanulaceae	2	2	2
Caryophyllaceae	4	2	1
Coriariaceae	1	1	1
Ericaceae	12	5	5
Fabaceae	8	8	3
Gentianaceae	7	4	1
Geraniaceae	4	3	1
Lamiaceae	2	2	2
Loganiaceae	2	2	1
Melastomataceae	5	5	3
Onagraceae	7	5	2
Oxalidaceae	3	3	3
Passifloraceae	1	1	1
Plantaginaceae	3	3	3
Polygonaceae	3	3	3
Rosaceae	14	13	12
Rubiaceae	2	1	1
Saxifragaceae	4	3	3
Scrophulareaceae	9	7	6
Valerianaceae	8	6	3
Vitaceae	1	1	1
Total	214	157	107

paired t-test using the 20 categories of plants found in both the faecal dietary analysis and the habitat transects gives a value of 1.32 ($P > 0.05$). This indicates that the mountain tapir is selecting certain favoured plants regardless of their relative abundance in its habitat. Summarized results of the vegetative transects, dietary items, and taxa germinating from tapir faeces can be found in Downer (1996*a*).

Microhistological dietary analysis

Flower parts were noted in five of the 37 samples. These displayed a low combined index from the faecal analysis (Table 3). There was one case of two combined Rosaceae genera, *Acaena–Alchemilla*, because they could not be distinguished under the microscope. The results for these 40 categories allowed a quantitative ranking among dietary items and permitted a comparison of field transect *vs* faecal analysis presences for the 20 groups that occurred in both (Table 2). This also permitted the calculation of preference ratios (Table 2).

Table 2. Preference ratios (PR), germination frequencies (GF), and related indices for food items in mountain tapir *Tapirus pinchaque* dietary analysis. B (beta value), relative proportion of food item in tapir's diet (from faecal analysis); A (alpha value), relative proportion of food item in habitat (from transects); PR = B/A. PR > 1 is 'preferred', while PR < 1 is 'avoided' (Jacobs, 1974); GF, number of separate observations counting only one per faecal sample whether in faecal germination experiment or as observed in the field. Culebrillas sector, Sangay National Park, Ecuador, 1990-93. Original figures rounded to hundredth decimal place. NO = not observed

Food item	B	A	PR	ln *e* PR	GF
Lupinus	3.47	0.25	13.79	2.62	44
Gynoxys (outlier)	24.37	3.15	7.74	2.05	55
Equisetum	8.10	1.23	6.61	1.89	52
Stachys	1.32	0.24	5.41	1.69	28
Brachyotum	6.24	1.75	3.56	1.27	47
Oreopanax	1.62	0.47	3.48	1.24	NO
Bromus	1.14	0.41	2.76	1.02	23
Ferns	19.43	7.19	2.70	0.99	NO
Gunnera	5.57	3.94	1.41	0.34	46
Lasiocephalus	1.66	1.20	1.39	0.33	NO
Calceolaria	2.65	1.99	1.33	0.29	39
Jungia	0.75	0.68	1.10	0.09	NO
AcaenaAlchemilla	1.65	2.29	0.72	−0.33	37
Rubus	0.17	0.36	0.46	−0.78	19
Carex	1.96	4.98	0.39	−0.94	34
Ericaceae	0.74	2.43	0.30	−1.20	31
Neurolepis	1.07	5.77	0.19	−1.66	27
Luzula	0.28	1.61	0.17	−1.75	NO
Cortaderia	0.87	5.48	0.16	−1.83	18
Buddleja	0.15	2.37	0.06	−2.81	10
Gamochaeta	3.22	NO	NO	NO	40
Trifolium	0.14	NO	NO	NO	30
Total no. of items	22	20	20	20	17

Product–moment correlation coefficient for GF and ln *e* PR = 0.75 ($P < 0.01$, $n = 15$. $v = 13$) (see Fig. 1). Product–moment correlation coefficient for GF and PR = 0.57 ($P > 0.05$, $n = 15$, $v = 13$). Product–moment correlation coefficient for GF and B without outlier = 0.86 ($P < 0.01$, $n = 16$, $v = 14$) (see Fig. 2). Product–moment correlation coefficient for GF and B with outlier = 0.70 ($P < 0.01$, $n = 17$, $v = 15$) (Rohlf & Sokal, 1981: table 25)

Abundance of food in habitat types

By comparing the results from vegetative transects with those from a faecal dietary analysis conducted using 37 faecal samples, tapir food preferences were compared for the five habitat types in the study area. Analysis by single-classification analysis of variance (Sokal & Rohlf, 1981) showed no significant difference ($P > 0.05$) among the five habitat types in food preferences, when values for all transects were compared to the average value for each habitat type. However, a ranking based on available preferred food produced the following order: (1) chaparral, (2) Andean forest, (3) paramo, (4) pampas, (5) riverine meadow (Table 4).

Table 3. Food items identified by microhistological examination (dietary composition analysis) of faecal samples ($n = 37$) of mountain tapir *Tapirus pinchaque*, with relative density and percentage, frequency and percentage, and combined index (sum of two preceding percentages) for each food item as sorted in descending order of combined indices. Culebrillas sector, Sangay National Park, Ecuador, 1990–93

Food item	Relative density	%	Frequency	%	Combined index (% + %)
Gynoxys	1451.64	39.23	35	9.51	48.74
Ferns	1076.23	29.08	36	9.78	38.86
Equisetum	317.95	8.59	28	7.61	16.20
Brachyotum	139.78	3.78	32	8.70	12.48
Gunnera	100.17	2.71	31	8.42	11.13
Lupinus	65.61	1.77	19	5.16	6.93
Gamochaeta	127.23	3.44	11	2.99	6.43
Unknown forb II	81.60	2.21	13	3.53	5.74
Calceolaria	14.88	0.40	18	4.89	5.29
Unknown forb I	29.03	0.78	16	4.35	5.13
Festuca	10.15	0.27	15	4.08	4.35
Carex	44.45	1.20	10	2.72	3.92
Lasiocephalus	12.18	0.33	11	2.99	3.32
Acaena–Alchemilla	51.35	1.39	7	1.90	3.29
Oreopanax	9.12	0.25	11	2.99	3.24
Stachys	26.93	0.73	7	1.90	2.63
Bromus	4.11	0.11	8	2.17	2.28
Munnozia	50.49	1.36	3	0.82	2.18
Neurolepis	8.77	0.24	7	1.90	2.14
Cortaderia	3.56	0.10	6	1.63	1.73
Jungia	5.31	0.14	5	1.36	1.50
Ericaceae	4.17	0.11	5	1.36	1.47
Flower parts	3.89	0.10	5	1.36	1.46
Eleocharis	30.41	0.82	2	0.54	1.36
Unknown forb	4.76	0.13	3	0.82	0.95
Moss	1.04	0.03	3	0.82	0.85
Hypochoeris	0.95	0.03	3	0.82	0.85
Juncus	11.12	0.30	2	0.54	0.84
Gaidendron	3.41	0.09	2	0.54	0.63
Arthropod parts	0.88	0.02	2	0.54	0.56
Luzula	0.79	0.02	2	0.54	0.56
Grass seed	0.67	0.02	2	0.54	0.56
Rubus	2.20	0.06	1	0.27	0.33
Unknown forb III	1.60	0.04	1	0.27	0.31
Composite I	1.31	0.04	1	0.27	0.31
Agrostis	0.64	0.02	1	0.27	0.29
Buddleja	0.59	0.02	1	0.27	0.29
Trifolium	0.43	0.01	1	0.27	0.28
Satureja (type)	0.41	0.01	1	0.27	0.28
Muhlenbergia	0.19	0.01	1	0.27	0.28
Total	3700.00	99.99%	368	99.98%	199.97

Preference ratios

A preference ratio is illustrated in Table 2 and in Downer (1996*a*), for each of the 20 coinciding faecal dietary and transect values. Some notable results are as follows:

(1) *Lupinus* (Leguminosae) is clearly selected. This is apparent because of its relative scarcity in the habitat (alpha = 0.25) and its relatively large dietary presence (beta = 3.47). The preference ratio of 13.79 represents the highest value registered (Table 2).

(2) A common silver-green leafed tree of the genus *Gynoxys* (Asteraceae) is the most abundant food item with a combined index from faecal analysis of 48.74 (Table 3). Although common, its habitat abundance is less than its dietary abundance resulting in a high preference ratio (7.74; Table 2). Although ferns were much more abundant in the habitat than *Gynoxys*, with an alpha value of 7.19, *Gynoxys* was preferentially chosen over ferns.

(3) Among the 40 food items in Table 3, ferns occur most frequently in the habitat (Table 2) and constitute the second most common dietary item, with a combined index from the faecal analysis of 38.86. Known ferns eaten included *Blechnum loxense* and *Thelypteris* spp. Although fern sporelings were present in the germination experiments, they could not be precisely identified to genus or species levels.

(4) Another noteworthy food is the *Oreopanax* tree, whose habitat frequency was 0.47 and whose dietary

Table 4. Mountain tapir *Tapirus pinchaque* food ranking among five habitat types, determined by summing identified foods' average coverage percentages and frequency percentages, as determined by transects (range 2–3) conducted in each habitat type, to obtain a combined index. Culebrillas sector, Sangay National Park, Ecuador, 1990–93

Habitat type	Coverage (%)	Frequency (%)	Combined index	Food rank
Chaparral	55.82	53.57	109.39	1
Andean forest	45.52	48.32	93.84	2
Paramo	40.38	47.70	88.08	3
Pampas	33.65	54.34	87.99	4
Riverine meadow	50.04	37.93	87.97	5
Average for 5 types	45.08	48.37	93.45	

frequency was 1.62. In this instance, a preference ratio of 3.48 is here considered strongly preferred.

(5) Common in riverine meadow, the mint *Stachys*, with a preference ratio of 5.41, provides an example of an occasionally encountered plant being strongly selected by the mountain tapir. The common bush *Brachyotum* (Melastomataceae) is similarly preferred, with a preference ratio value of 3.56. Both juvenile and adult tapirs were observed to eat this bush (Castellanos-Peñafiel, 1994).

(6) Ferns and the grass genus *Bromus* had about the same preference ratios (2.76, Table 2). *Bromus* was unusual in being one grass that was selected in greater quantity than its documented presence in the habitat of the mountain tapir.

(7) With preference ratio values of 0.16 and 0.19, respectively, the common grass genera *Cortaderia* (alpha = 5.48) and *Neurolepis* (alpha = 5.77) were not frequently consumed although they were often present.

(8) With a preference ratio of 1.41, another common genus, *Gunnera*, was only slightly preferred, perhaps because of its considerable habitat abundance. This included the umbrella plant, *Gunnera brephogea*, which the mountain tapir also uses for shelter (Downer, 1996*b*,*c*). The fallen, decomposing trunk as well as leaves of this species are frequently eaten by mountain tapirs.

Germination of seeds from mountain tapir faeces

Laboratory experiments, field observations, and other sources demonstrate that many taxonomically diverse species germinate from tapir faeces (Appendices 1 & 2). Eighty-six (42%) of 205 vascular plant species eaten by mountain tapirs in the study area germinated through their faeces (Downer, 1996*a*: 50–51, table 1). This represented 32.6% of those 264 species of tracheophytes recorded in the habitat. Fifty-three tracheophyte genera (40.5% of 131 total) are dispersed by mountain tapirs. Among 57 tracheophyte families documented to occur in the study area, 29 (54.7%), nearly all dicotyledons, had species that germinated through mountain tapir faeces (Downer, 1996*a*: 50–51, table 1). The results of germination experiments (Appendix 1) substantiated the quantity of species being dispersed by the mountain tapir as determined in the field (Appendix 2).

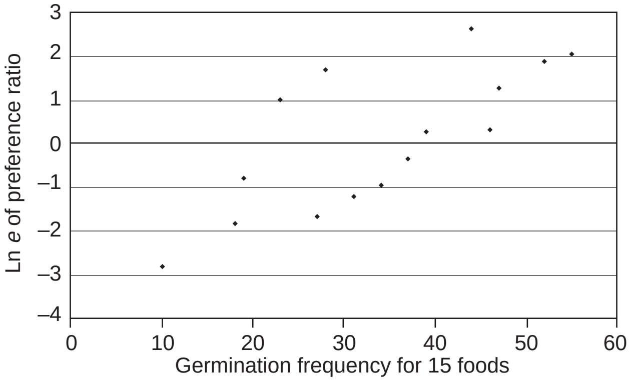

Fig. 1. Scatter plot of the natural logarithm (ln *e*) of preference ratio and germination frequency correlation ($n = 15$) for the mountain tapir *Tapirus pinchaque*, Sangay National Park, Ecuador (see Table 2).

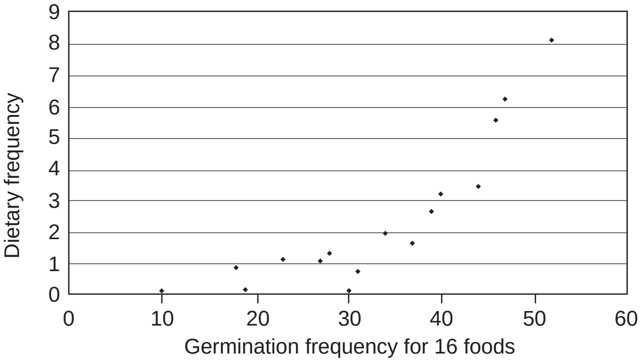

Fig. 2. Scatter plot of dietary and germination frequencies correlation with outlier removed ($n = 16$) for the mountain tapir *Tapirus pinchaque*, Sangay National Park, Ecuador (see Table 2).

An index of mutualism

A highly significant correlation ($P < 0.01$, $r = 0.75$, $n = 15$, $v = 13$) exists between the ln *e* of preference ratios and the germination frequency of 15 plant food items (Fig. 1, Table 2). Also highly significant ($P < 0.01$, $r = 0.86$, $n = 16$, $v = 14$) is the direct correlation between the dietary frequency and the germination frequency of 16 plant food items excluding the outlier *Gynoxys* (Fig. 2, Table 2) as well as the same correlation including the outlier ($P < 0.01$, $r = 0.70$, $n = 17$, $v = 15$). Other correlations (see Materials and methods) proved non-significant (Table 2) (Rohlf & Sokal, 1981: table 25).

DISCUSSION

Feeding type and preference and relationship with sympatric herbivores

The fact that there was no statistically significant, positive correlation between the habitat abundance of dietary plants and their frequency in the diet of the mountain tapir indicates that this herbivore is a selective browser that chooses certain favourite foods. The high preference ratio for certain nitrogen fixers such as *Gunnera* and *Lapinus* may relate to their higher nitrogen content (Bentley & Johnson, 1991). The low preference ratios for grasses (Table 2) and the observed abundance of leaf remains in the faeces confirms that the mountain tapir is primarily a foliose browser rather than a grass grazer (Frädrich, 1970) and suggests an ecological compatibility with the three ruminant deer species found in the study area (Downer, 1996*a*). Although *Mazama rufina* is known to select ripe, fallen fruit (D. Brooks, pers. comm.) in tropical forest, generally ruminant grazers consume less coarse vegetation emphasizing young, low-fibre grass blades and similar forage types when compared with post-gastric grazers such as the mountain tapir (Bell, 1971; Janis, 1976). Further study of niche overlap among these herbivores could prove revealing.

Ecological role of tapirs

The mountain tapir may well act as a keystone species, as a result of its seed dispersing capabilities, in the Sangay National Park region and elsewhere in the mid to high elevational, northern Andes. A large portion of the original high Andean flora from northern Peru northward could depend upon the mountain tapir as a seed disperser; and goodness-of-fit tests comparing the geographical distributions of plant species and mountain tapirs would provide interesting results. For example, Colombia's national tree, the Quindean wax palm *Ceroxylon quindiuense*, may be greatly dependent upon the mountain tapir for successful reproduction (J. Cavelier, H. Acosta & E. Londoño, pers. comm.), and its survival may be jeopardized if the mountain tapir becomes extinct. The Quindean wax palm is an important food source for vertebrate species, particularly birds such as high altitude parrots that nest in its fronds (pers. obs.).

The important role that the mountain tapir plays as a seed disperser in the high Andean ecosystem (Appendices 1 & 2) is comparable to information on the Baird's tapir (Janzen, 1982; Williams, 1984). The other lower-dwelling species of tapir, *T. indicus* (Medway, 1974; Williams, 1978, 1979) and *T. terrestris* (Bodmer & Brooks, 1997), also act as seed dispersers for many rain forest plant species (Williams & Petrides, 1980; Janzen, 1982; Bodmer, 1989, 1991). Because the high Andean ecosystem occupied by the mountain tapir is much less complex botanically and faunistically than a lowland rain forest (Patzelt, 1985; Gentry, 1991; Ramsay, 1992), this endangered tapir may fill an even more crucial ecological role here than does its lowland congener, *T. terrestris*, within lowland forests (Bodmer & Brooks, 1997). Other large seed dispersers are scarce when compared with the lowland forest (Ortiz Von Halle, 1991; D. Brooks, pers. comm.).

While no data are presented here, the mountain tapir seems to play a significant role in volcanically active areas. For example, tapirs that reoccupy the Culebrillas area after volcanic eruptions depositing ash or cinder, could serve to reconstitute the ecosystem through their seed-dispersing ability (A. Bolivar Colonel, pers. comm.). This is an important consideration in deciphering the evolutionary past of the mountain tapir in the volcanically active Andes, and deserves serious study, as would be possible in the recently volcanically denuded slopes around Tungurahua Volcano, at the northern tip of Sangay National Park.

Mutualism between mountain tapir and high Andean flora

Members of Tapiridae serve as surrogate dispersers for fruiting plants formerly dispersed by Pleistocene megafauna. Species including many native South American notoungulates and lipoterns became extinct with climatic changes occurring at the re-establishment of the Panamanian Isthmus and to some extent because of the resultant competition from northern species (Eisenberg, 1981; Janzen & Martin, 1982).

The line of evolutionary descent leading to the mountain tapir's current occupation of the mid to high elevational northern Andes probably dates from the re-establishment of the Panamanian Isthmus uniting Central America with South America during the Pliocene epoch *c.* 3 million years before present. Evidence suggests that the Isthmus permitted tapirs to occupy South America (Webb & Marshall, 1982) and that a single common ancestor of *T. pinchaque* and *T. terrestris* crossed the Isthmus at this time (Ashley, Norman & Stross, 1996).

The highly significant correlations for the faecal germination frequencies of mountain tapir food items and both their dietary frequencies and their ln *e* of preference ratios support a mutualism between the mountain tapir and many of the plants it eats. These correlations substantiate the critical seed disperser role that *T. pinchaque* has probably played in the evolution of the mid to high northern Andean ecosystem. Perhaps some of these mutualisms were initially formed at lower elevations when the ecosystem had a more temperate climate during glacial periods (Hershkovitz, 1954), or before the spectacular and geologically recent Andean rise since the Quaternary Period (late Cenozoic) *c.* 2.5 million years before present (Simpson, 1979;

Benton, 1991). Perhaps some of these evolved in the mid to high elevational Andes themselves. Studies of seed dispersal among other herbivorous species sympatric with the mountain tapir would reveal their relative ecological importance and provide an important test for my hypothesis.

It is possible that the direct-line ancestry of the mountain tapir synchronically co-evolved with a variety of plant species as the Andes rose and new habitats were formed. This young mountain range attained elevations above 2000 m since *c.* 2 million years before present (Simpson, 1979; Ortiz Von Halle, 1991) after the Panamanian Isthmus connected Central and South America and the entrance of the possible shared ancestor of *T. pinchaque* and *T. terrestris* (Ashley *et al.*, 1996) to South America. Because 2000 m is the approximate lower elevational limit of the mountain tapir (Schauenberg, 1969; Baillie & Groombridge, 1996), this tapir's ancestors possibly established the current mid to high Andean niche of the present mountain tapir during the past 2–3 million years, since their crossing of the Panamanian Isthmus. Since the beginning of the heavily glacial Pleistocene epoch and along with other mid and high elevational Andean flora and fauna, the mountain tapir has probably adapted to survive by adhering to colder temperatures at increasing elevations as lower elevations warmed (Hershkovitz, 1954).

Providing additional corroboration of the foregoing, the 2000 m elevation is noted as the tree line during the coldest period of the last glacial (Van Der Hammen, 1974). The deforestation of Andean habitats above this elevation or close elevations during preceding glacial ages may have provided unoccupied habitat for the mountain tapir, similarly to volcanic eruptions. This may have caused a genetic separation from the lowland tapir on the Amazonian side because of the strikingly different environmental conditions between highlands and lowlands. Although the two congeners are occasionally noted as sympatric on the eastern slopes of the eastern Andes of both Colombia (Hershkovitz, 1954) and Ecuador (L. Albuja & P. Mena, pers. comm.; pers. obs.), where they are rumoured to interbreed, this is definitely more the exception than the rule, probably as a result of genetic differences, including furriness and heat intolerance. The mountain tapir is more closely related to *T. terrestris* than to any of the other extant species, as determined by shared characters (Hershkovitz, 1954) and genetic analysis (Ashley *et al.*, 1996).

The lowest natural elevational limit at which the mountain tapir has been reported is *c.* 1400–1500 m (Cuvier, 1829; Roulin, 1829; Goudot, 1843; L. Albuja & P. Mena, pers. comm.; pers. obs.). This elevation marks the transition between: (1) the lower Amazon forest, where a considerably greater species diversity prevails, and (2) the mid to high Andean cloud forests, where a lesser degree of species diversity exists (Gentry, 1991). Evidence suggests that the mountain tapir is obligatorily co-adapted to the latter zone (Schauenberg, 1969).

If the lowland tapir was not already a distinct species, perhaps the abrupt rise of the Andes coupled with global warming led to speciation and separation of this close relative from the cold, higher montane-adapted mountain tapir, which is considered less phylogenetically derived (Hershkovitz, 1954). A recent detailed phylogenetic analysis of the four extant tapirs using mitochondrial cytochrome-*c* oxidase (COII) 'indicate a close relationship between the two exclusively South American species of tapirs, *T. terrestris* and *T. pinchaque*, and estimates of divergence dates using rates of COII evolution are compatible with migration of a single tapir lineage into South America following the emergence of the isthmus of Panama, about 3 million years before present (Ashley *et al.*, 1996: 315).

Mountain tapir survival is considered a crucial factor for the conservation of northern Andean wilderness and watershed. This umbrella species has a large home range (880 ha) and minimally viable area (293 500 ha) (Downer, 1996*a*), and its salvation will insure that of many sympatric species. Without this species, a substantial portion of the native Andean flora is reproductively impeded. As a consequence, soils and watersheds fail to form in their accustomed manner, contributing to ecological disintegration affecting highlands and lowlands alike. But if humans can learn to appreciate, conserve, and restore this ancient, *c.* 3-million-year Andean survivor in heeding its more harmonious mutualistic lifestyle, then a more promising future may lie in store for us all.

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Appendix 1. Identified[a] genera and species germinating from mountain tapir *Tapirus pinchaque* faeces as determined by faecal germination experiments at the Instituto Nacional de Investigacion Agropecuario, Quito, Ecuador, 1991–92, with taxonomic identifications at Missouri Botanical Garden Herbarium. Sangay National Park, Ecuador.

- Kingdom, Plantae
- Nonseeding plants
- Division Bryophyta (identified by M. Lewis)
- Class Muscopsida (mosses)
  - *Bryum argenteum* E
- Class Hepaticopsida (liverworts)
  - *Frullania hygrometrica* E
  - *Marchantia* sp. E
- Division Tracheophyta (vascular plants)
- Class Sphenopsida (identified by R. Moran)
- Family Equisetaceae (horsetails)
  - *Equisetum bogatense* E O
- Subdivision (or class) Angiospermae (flowering vasculars)
- Class Liliopsida (or subclass Monocotyledoneae)
- Family Cyperaceae (sedges) (identified by G. Davidse)
  - *Carex* sp. E
  - *Eleocharis acicularis* E O
  - *Scirpus inundatus* E
- Various unknown sedge species germinating in experiment
- Family Gramineae (Poaceae) (identified by G. Davidse)
  - *Eragrostis tenuifolia* E
  - *Eragrostis* sp. E
  - *Paspalum prostratus* E
  - *Poa annua* E
  - *Poa* sp. E
  - *Triticum aestivum* E
- Class Magnoliopsida (or subclass Dicotyledoneae)
- Family Amaranthaceae (identified by T. Borsch)
  - *Amaranthus hybridus* E
- Family Asteraceae (identified with aid of R. Leisner)
  - *Baccharis* sp. E
  - *Cotula mexicana* E
  - *Erechtites hieracifolia* E
  - *Galinosoga quadriradiata* E
  - *Gamochaeta americana* E
  - *Gamochaeta purpurea* E
  - *Gynoxys* cf. *buxifolia* E O
  - *Taraxacum officinale* E O
- Various unknown aster species germinating in experiment
- Family Caryophyllaceae (identified by R. E. Gereau)
  - *Cerastium glomeratum* E
- Family Fabaceae (legumes)
  - Unknown species E
- Family Lamiaceae (mints)
  - *Stachys elliptica* E O
- Family Oxalidaceae (sorrel)
  - *Oxalis lotoides* E O
- Family Plantaginaceae (plantain)
  - *Plantago australis* E O
- Family Polygonaceae (buckwheat)
  - *Rumex tolimensis* E O
- Family Rosaceae (identified by R. E. Gereau)
  - *Prunus serotina* E O
- Family Scrophulariaceae (identified by R. Leisner)
  - *Veronica peregrina* E
- Family Solanaceae (identified by B. D'Arcy)
  - *Nicandra physalodes* E

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[a] E, evidence from faecal germination experiments; O, corroborative evidence from field observations.

All identifications checked by Dr Ron Leisner or other named botanists at Missouri Botanical Garden Herbarium. Help also received from Catholic University Herbarium, Quito, Ecuador. Unidentified fern sporelings also produced during tapir faecal germination experiments.

Appendix 2. Identified[a] genera and species germinating from mountain tapir *Tapirus pinchaque* faeces as determined by field observation with taxonomic identification at Missouri Botanical Garden Herbarium. Sangay National Park and other Andean sites, Ecuador, 1989–95

Kingdom Plantae
Division Tracheophyta (vascular plants)
Class Sphenopsida (identified by R. Moran)
Family Equisetaceae (horsetails)
  Equisetum bogatense O E
Subdivision (or class) Angiospermae (flowering vasculars)
Class Liliopsida (or subclass Monocotyledoneae)
Family Bromeliaceae
  Greigia vulcanica O
  Puya sp. O
Family Cyperaceae (sedges) (identified by G. Davidse)
  Eleocharis acicularis O E
  Carex O E
Family Gramineae (Poaceae) (identified by G. Davidse)
  Bromus lanatus O
  Bromus pitensis O
  Cortaderia nitida O
  Cortaderia sp. O
  Neurolepis aristata O
  Neurolepis sp. O
Class Magnoliopsida (or subclass Dicotyledoneae)
Family Apiaceae (carrot)
  Arracacia elata O
  Arracacia tolucensis O
Family Asteraceae (identified with aid of R. Leisner)
  Gynoxys cf. *buxifolia* O E
  Taraxacum officinale O E
Family Campanulaceae
  Centropogon glaucotomentosum sp. aff O
  Centropogon ursinus O
Family Coriariaceae
  Coriaria ruscifolia spp.*microphylla* O
Family Ericaceae
  Ceratostema alatum O
  Disterigma empetrifolium O
  Pernettya prostrata O
  Vaccinium attenuatum O
  Vaccinium campanulatus O
Family Fabaceae (legumes)
  Lupinus caucensis O
  Trifolium cf. *dubium* O
Family Geraniaceae
  Geranium hirtum O
Family Halogoraceae (Gunneraceae)
  Gunnera magellanica O
Family Lamiaceae (mints)
  Satureja nubigena O
  Stachys elliptica O E
Family Loganiaceae
  Buddleja incana O
Family Melastomataceae
  Brachyotum alpinum O
  Brachyotum ledifolium O
  Miconia crocea O
Family Onagraceae
  Fuchsia vulcanica O
  Fuchsia aff. *vulcanica* pos nov sp. O
Family Oxalidaceae (sorrel)
  Oxalis lotoides O E
  Oxalis microphylla O
  Oxalis mollis O
Family Passifloraceae O
  Passiflora mixta O
Family Plantaginaceae (plantain)
  Plantago australis O E
  Plantago lanceolata O
  Plantago nubigena O
Family Polygonaceae (buckwheat)
  Rumex crispus O
  Rumex obtusifolius O
  Rumex tolimensis O E
Family Rosaceae (identified by R. E. Gereau)
  Alchemilla aphanoides O
  Alchemilla cf. *guatemalensis* O
  Alchemilla hispidula O
  Alchemilla orbiculata O
  Alchemilla spruceii O
  Alchemilla verticillata O
  Hesperomeles escalloniifolia O
  Hesperomeles pernettyoides O
  Polylepis quadrijuga O
  Rubus acanthophyllus O
  Rubus loxensis O
  Prunus serotina O E
Family Rubiaceae
  Galium hypocarpium O
Family Saxifragaceae
  Ribes andicola O
  Ribes cf. *cuneifolium* O
  Ribes cf. *lehmannii* O
Family Scrophularaceae (identified by R. Leisner)
  Calceolaria adenanthera O
  Calceolaria calycina O
  Calceolaria ferruginea O
  Calceolaria parotrichia? O
  Calceolaria spruceana O
Family Valerianaceae
  Valeriana microphylla O
  Valeriana plantaginea O
  Valeriana pyramidales? O
Family Vitaceae (wild grape)
  Cissus cf. *andina* O

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[a] E, evidence from faecal germination experiments; O, corroborative evidence from field observations.

All identifications checked by Dr Ron Leisner or other named botanists at Missouri Botanical Garden Herbarium. Help also received from Catholic University Herbarium, Quito, Ecuador. Unidentified fern sporelings also produced during tapir faecal germination experiments.